orient the core proteins, but this then serves as a mechanism to polarise cilia. Ciliary beating can then generate mechanical forces, which in turn can play their own roles in defining or refining cell polarity. It will be interesting to see in what other contexts this reciprocal interaction between mechanical forces and planar polarity plays an important role.

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Neuroethology: Unweaving the Senses of Direction

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Three recent studies have significantly advanced our understanding of the highly conserved central complex of the insect brain, showing how it provides an internal representation of body orientation, encodes behaviorally relevant sensory cues, and at the same time controls motor actions.

You have to know which direction you are facing to decide where to go next. This is true for us when we stare at a topographical map, trying to spot the unmarked trail to that mountain lake, only to realize that our compass is hiding way back in the glove compartment of the car. It is also true for our six-legged friends: the tiny fruit fly that, within minutes, pinpoints the glass of Sauvignon Blanc in the middle of your apartment; the bulky dung-beetle that, tank-like, rolls its favorite poo-ball in a straight line across the African savanna, slow, steady, backwards, eyes fixed on the sky; and the sleek cockroach that well, who knows what roaches do, but they certainly do it speedily, with determination. But how do insects know the direction they are facing? And how do they then select the direction into which to move next? The answers lie in their brain; as yet we do not know what they are, but significant progress has been made by three recent studies [1–3]. Seelig and Jayaraman [1] have tracked down the fly's sense of direction to a defined brain area; el Jundi *et al.* [2] have uncovered how the same brain area keeps dung beetles robustly oriented to maintain a straight course; and, as reported in this issue of *Current Biology*, Martin *et al.* [3] have revealed how this region governs the next move of a cockroach. All three papers combined behavioral experiments with functional studies of a highly conserved region of the insect brain, the 'central

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complex'. By using the unique advantages of each species these studies also remind us about the benefits of classic neuroethology.

What do we know about the central complex? It is the only unpaired region of the insect brain; it is located in the center of the brain; and it is composed of highly interconnected modules [4]. Its overall configuration is conserved across all insects and it exhibits a characteristic intrinsic layout. An array of vertical slices of ordered neural tissue, intersected by several horizontal layers, gives this neuropil an appearance of almost crystalline regularity. This layout is generated by sets of repeating neural elements (columnar and tangential cells), whose complex inter-hemispheric, reverberating connectivity patterns have made it extremely difficult to predict principles of information flow within this neuropil [5,6].

But why should we care? Because of what brains do in general. One of the main functions of all brains is to take sensory information, use it to generate an estimate of the current state of the world, and then compare it to the desired state of the world. If the two do not match, compensatory action is initiated, which is what we call behavior. Computing the desired state of the world depends on the internal state of the animal (for example, its hunger-level or reproductive status), on previous experience, and the current behavioral context. The central complex is involved in many of the required processes, such as sensory mapping [7], initiation of behavior [8], context-dependent sensory encoding [9], neuromodulation [10], and visual and spatial memory [11–13] — a long list of fundamental brain functions. How all these features are put together into a coherent picture has puzzled researchers for nearly two decades. We can simplify this task by focusing on the first half of the story: for the brain to make sense of a desired state of the world, it has first to encode the current state of the world, a task that can essentially be reduced to the questions of 'where am I in relation to my environment?' and 'what in this environment is relevant for me?'. It is within this context that we are beginning to understand the role of the central complex.

In the first of the three new studies, Seelig and Jayaraman [1] genetically expressed a calcium sensor in a specific set of central-complex neurons of the fruit fly *Drosophila*. Whenever these neurons fired action potentials, the sensor would change its fluorescence levels. This was in turn detected by a two-photon microscope viewing the fly's exposed brain. At the same time, the fly was mounted on a tiny, air-suspended styrofoam ball, allowing it to walk freely in all directions without leaving its position. The rotations of the ball generated during walking were then fed back to a panoramic LED display, leaving the fly with the impression that changes in its walking direction trigger matching changes of the visual scene. The monitored neurons were a set of 16 columnar cells, each with a dendritic field in one radial slice (a 'wedge') of the ellipsoid body (one central-complex module), with all 16 wedges together filling the full circular range of the ellipsoid. When the fly faced an arbitrary visual scene, the activity within this neuron population converged in a single activity bump (Figure 1). Whenever the fly changed its orientation relative to the visual panorama, this bump moved accordingly. Importantly, the bump's location was independent of the structure of the visual scene. Moreover, while consistent within a trial, the absolute position of the activity bump varied randomly between individual flies. Thus, no information about the actual structure of the environment is present in these neurons. Rather, they indicate the fly's heading angle with respect to the visual panorama in a relative, self-centered reference frame, a behavior that is highly reminiscent of mammalian head-direction neurons: these head direction cells not only respond to visual cues in the environment, but also strongly rely on self-generated cues, for example, those resulting from changes in body posture, leg position and so on [14].

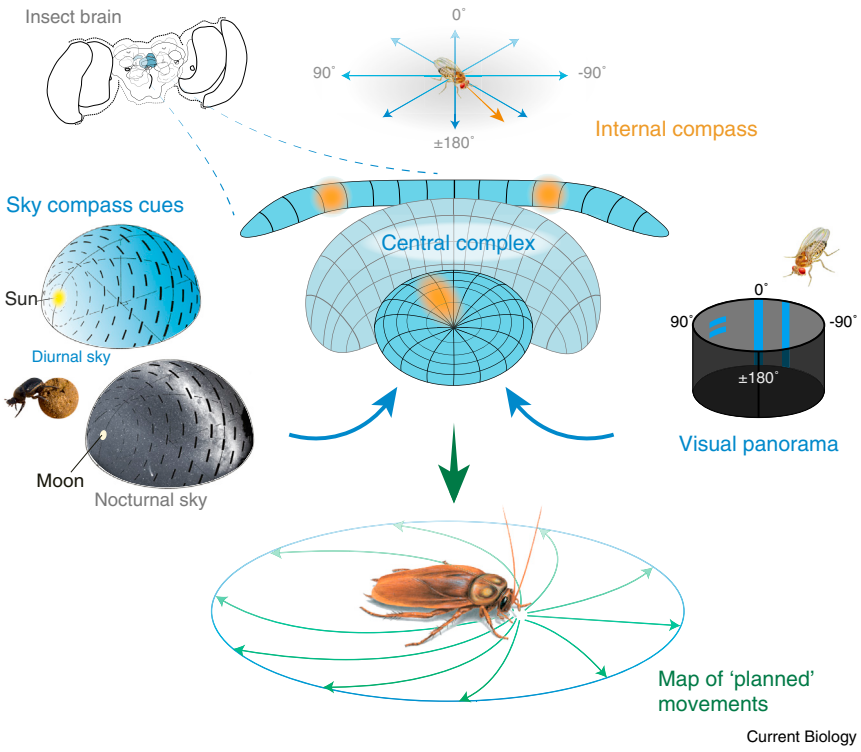

Figure 1. Insights into central-complex function based on recent work in *Drosophila* [1], dung beetles [2] and cockroaches [3].
Diurnal and nocturnal skylight compass cues (dung beetles) and information about the visual panorama (*Drosophila*) are channeled towards the central complex. In *Drosophila*, a single activity bump (orange) is generated in the ellipsoid body that corresponds to the heading angle of the fly. This head direction signal is relayed to the protocerebral bridge (topmost structure), the location of a polarized-light-based direction map in locusts. These direction maps can serve as a reference frame for initiation of behavior. In cockroaches (bottom), a neuron population representing the imminent movements of the animal has been found. Shown are schematic trajectories of the animal predicted from the activity of central-complex neurons. Sky images reproduced with permission from [18]. Beetle image: Basil el Jundi.

Can the *Drosophila* wedge-neurons hold up to the mammalian standard? Indeed they can — when no visual cues were present and the fly was walking in darkness, the cells also generated a persistent activity bump that corresponded to the fly's heading. These results indicate that a system of 16 columnar wedge-neurons in the *Drosophila* ellipsoid body serves as an internal compass that combines self-generated cues with visual landmarks, and which is recalibrated in each new environment. Interestingly, these wedge-neurons systematically project to the protocerebral bridge, another central-complex compartment. In locusts, this region contains an ordered array of polarized-light-based direction cells [7]. Unlike in the fly, the locust cells' directional tunings appear to be stable across individuals and provide these migratory insects with a global, sun-based reference frame. Despite these differences, which might be ascribed to the species' different behavioral strategies, it is remarkable that the central complex comprises an internal reference frame across insects separated by several hundred million years of evolution.

What would these neurons do in a species with an entirely different behavior? el Jundi *et al.* [2] examined the same cells in African dung beetles, using intracellular electrophysiology. These beetles are as equally opportunistic as flies when locating their food (a pile of fresh dung), but they show a unique behavior once on the ground. After finding their dung, they shape a small portion of it into a ball and roll it away as fast as they can to avoid the fierce competition from other beetles. The fastest escape strategy is to simply roll in a straight line, which is exactly what these beetles do. A wealth of behavioral data have revealed that, unlike flies, ants, or bees, dung beetles ignore landmarks, but rather rely on a variety of skylight compass cues to keep a straight course [15]. Interestingly, this is equally true for closely related nocturnal and diurnal species, with one essential difference: although both can use the currently present celestial body (sun or moon) and the skylight pattern of polarized light, they weight these cues differently.

With elegant behavioral experiments, el Jundi *et al.* [2] showed that, during their natural foraging hours, the nocturnal species prefers to use the polarization pattern, whereas the diurnal species relies on the sun. Then the authors forced the beetles to roll their balls during the wrong time of day — during daylight hours for the nocturnal species, and during the night for the diurnal species. While the day-active species stuck to its preference for the celestial body and used the moon as reference, the nocturnal species now ignored the polarized light pattern and instead relied on the sun. This means that the nocturnal species switched its cue preference from night to day, whereas the day-active species did not.

Given that we know that central-complex neurons respond to visual compass signals, el Jundi *et al.* [2] hypothesized that the differences in behavioral preference of the two species might be governed by central-complex neurons. After identifying a compass network in beetles highly similar to the one found in locusts and monarch butterflies [16], they studied two sets of neurons in detail, one of which is homologous to the *Drosophila* wedge-neurons. By simulating the natural conditions during the day and night in the recording setup, the authors tested how strongly the neurons would respond to each skylight cue individually and during combined presentation. Remarkably, the relative strength of stimulus responses during the neural recordings exactly predicted the results of the behavioral experiments. Because the stimuli encoded in the central complex match the stimuli to which the beetles respond to behaviorally, it is conceivable that these compass neurons might control orientation behavior. But is there really a causal link between the neural firing in this brain region and the insect's motor actions?

The third paper, by Martin *et al.* [3], sheds light on this question. The authors inserted flexible, twisted-wire electrodes into the cockroach central complex and recorded extracellular action potentials while the animals were freely exploring an arena. This difficult, but extremely powerful setup allowed them to correlate the recorded signals to the ongoing natural behavior. Indeed, the majority of recorded cells showed activity that strongly depended on the animal's walking speed and turning tendency (angular velocity). But not only did these neurons correlate with the ongoing behavior, the majority of them actually fired most strongly just *before* initiation of a movement. When the authors analyzed the firing patterns more closely, they found that each neuron predicted a particular combination of future rotational and translational velocity. This means that the movement trajectory of an animal could be predicted from neural activity in the central complex. Across all recorded cells, the end points of these trajectories covered the complete space around the cockroach (Figure 1); this neuron population therefore encodes all possible imminent movements of the animal.

The central complex thus contains not only sensory maps and direction cells, but also a map of movement directions. But does this neural activity really cause the predicted movements? The beauty of the method used is that one is not only able to record from neurons, but also use the same wires to electrically stimulate the tissue around the electrode. When Martin *et al.* [3] did that, the cockroaches initiated highly defined, reproducible movements. The velocity components of these real trajectories were significantly correlated with the velocities that had been predicted from the recorded activity at the stimulation site, demonstrating a causal relation between the neural firing and the animal's movement.

How could activity in the central complex make the animal turn? Six legs have to be redirected in a coordinated manner at high speed to achieve the transition from straight running to a right or left curved turn. To investigate this question, Martin *et al.* [3] looked into the peripheral reflex circuits underlying walking, while electrically stimulating the central complex. When stimulating at a site that initiated turning, one particular reflex indeed switched its polarity. This reversal had been shown earlier to redirect leg-force in a way required for a sidewards movement [17], and it was not observed during stimulations at sites that caused only straight walking. As this reflex circuit was studied in isolation from the normal feedback mechanisms in place during walking, the observed modulation is likely a direct result of central-complex output acting via descending pathways. This is remarkable, as the paper [3] not only establishes the existence of a map of

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movement directions in the insect brain, it also closes the gap between this central representation and the implementation of the encoded movements at the level of motor neurons.

So, in the end, how do animals determine which direction they face and decide where to go next? If we combine the data from flies, beetles and cockroaches, assuming for a second that all insects are the same, we can infer an almost complete picture. Sensory information about the visual panorama and various compass cues are channeled to the central complex. This information is used to generate an ordered array of head-direction cells, which in flies closely resemble the characteristics of their mammalian counterparts, while in migratory locusts they constitute a global, sun-based compass. Dung beetles then tell us that the only sensory features encoded at the level of the central complex are those that are relevant to driving ongoing behavior. Finally, the work on the cockroach allows us to widen our focus from solely sensory representations and direction cells and include a full representation of movement trajectories, all within the neural substrate of the central complex. This offers a mechanism for how the animal initiates movement, and together with the two other papers it thereby paves a way towards finally asking the ultimate question about how animals make the *decision* about where to go next. How is the information about body orientation used to generate the newly identified representation of imminent movements? What other information is incorporated into this transformation process? These three remarkable papers show that scrutinizing the intricate structure–function relations of the insect central complex across diverse model species is likely to be one of the most promising approaches for understanding one of the most fundamental question of neuroscience: What are the neural algorithms that enable animals to make an appropriate behavioral choice when potentially faced with an infinite number of sensory scenarios?

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Evolution: Two (Very Long) Legs to Stand On

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How do the legs of jerboas get so long? A comprehensive study of the Dipodidae family of two-legged rodents reveals many evolutionary refinements in toe numbers, bone structures and proportions. Clearly, this adorable emerging developmental model system has legs.

Perched like a ball of fur on improbably large feet, sometimes sporting large Mickey Mouse ears, jerboas seem to be made for the age of viral internet videos. But the extreme proportions of this adorable mammal are more than buzzfeed or viral fodder. Rather, its long legs and sometimes large ears are the hallmarks of

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